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A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics

Sara B. Tavares[a,*], Filipa I. P. Samarra[a,b], Patrick J.O. Miller[a]

[a]Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, United Kingdom

[b]Marine Research Institute, Skulagata 121, Reykjavik, Iceland

[*]Address for reprint requests and correspondence: Sara B. Tavares, Sea Mammal Research Unit, School of Biology, University of St Andrews, Bute Building, St Andrews KY16 9TS, Scotland, United Kingdom. Telephone: +44 01334 463607. E-mail address: sbt3@st-andrews.ac.uk.

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ABSTRACT

Non-social factors can influence animal social structure. In killer whales (*Orcinus orca*), fish- vs. mammal-eating ecological differences are regarded as key ecological drivers of their multilevel society, including group size, but the potential importance of specific target prey

remains unclear. Here, we investigate the social structure of herring-eating killer whales in Iceland and compare it to the described social structures of primarily salmon- and seal-eating populations in the Northeast Pacific, which form stable coherent basic units nested within a hierarchical multilevel society. Using 29023 photographs collected over 6 years, we examined the association patterns of 198 individuals combining clustering, social network structure and temporal patterns of association analysis. The Icelandic population had largely weak but non-random associations, which were not completely assorted by known ranging patterns. A fission-fusion dynamic of constant and temporary associations was observed but this was not due to permanent units joining. The population-level society was significantly structured but not in a clear hierarchical tier system. Social clusters were highly diverse in complexity and there were indications of subsclusters. There was no indication of dispersal nor strong sex differences in associations. These results indicate that the Icelandic herring-eating killer whale population has a multilevel social structure without clear hierarchical tiers or nested coherent social units, different from other populations of killer whales. We suggest that local ecological context, such as the characteristics of the specific target prey (e.g. predictability, biomass and density) and subsequent foraging strategies may strongly influence killer whale social association patterns.

Key words: ecological context, hierarchical structure, multilevel societies, social structure, killer whale, orca

INTRODUCTION

The sociality of a group-living species is driven by a trade-off between its specific ecological, evolutionary and social contexts (Krause and Ruxton 2002). Non-social factors, particularly predation risk, finding/catching food, defending resources and resource patchiness, can strongly determine the social structure of simple social systems and provide the context for the development of complex ones (Jarman 1974; Wrangham 1980; Whitehead 2008a). General socioecological frameworks have been developed for various taxa, characterizing how such factors can affect sociality by using broad characteristics of a species/genera, such as occurrence of group foraging, group size or mating system (Emlen and Oring 1977; Wrangham 1980; Gowans et al. 2007). However, with the increase of within-species studies (e.g. Barton et al. 1996, Sinha et al. 2005; Whitehead et al. 2012), it seems clear that it is important to emphasize intraspecific variation which likely reflects variability under different ecological conditions. Investigating different populations of the same species across ecological gradients is therefore valuable to evaluate the influence of ecological drivers.

Multilevel societies are among the social systems found on group-living species and have been described as hierarchical structures of nested social levels (i.e. discrete social stratification of associations among individuals into tiers) with at least one stable core unit (Wittemyer et al. 2005; Grueter, Matsuda, et al. 2012; Grueter, Chapais, et al. 2012). Recently, de Silva and Wittemyer (2012) suggested that multilevel societies should be seen along a continuum of nestedness and that some might present less clearly hierarchically stratified social levels that transition more gradually. Commonly, multilevel societies exhibit fission–fusion dynamics, with frequent association, disassociation, and reassociation of

groups of individuals (e.g. Connor et al. 1992). Although multilevel societies have been studied more extensively in terrestrial mammals, particularly in primates (see Grueter, Chapais, et al. 2012), such social systems are also observed in cetaceans and intraspecific variation has been reported (Connor et al. 1998; Whitehead et al. 2012). For example, female sperm whales (*Physeter macrocephalus*) form long-term stable social units which, in the Pacific, temporarily group with other units with which they share part of the acoustic repertoire, but rarely group in the North Atlantic, possibly due to differences in predation risk (Whitehead et al. 2012).

One well-described tiered multilevel society among cetaceans is that of the 'resident' fish-eating killer whale (*Orcinus orca*) population in the Northeast Pacific, hereafter termed residents. The basic unit of this society is the matriline, consisting of an oldest surviving female and her philopatric descendants, remaining associated with their mother for life (Bigg et al. 1990; Baird and Whitehead 2000; Barrett-Lennard 2000). Within matrilineal units, individuals associate strongly and at very similar levels, while matrilineal units can frequently interact (Bigg et al. 1990; Baird and Whitehead 2000; Ford et al. 2000). Matrilines that share at least part of their acoustic repertoire, probably due to common maternal ancestry, form the next social level, the clan (Ford 1991). Different clans have no calls in common, and matrilines from the same or different clans frequently travel together (Ford 1991). The next and broadest social level (just under population) is the community, consisting of matrilines that share a common area and associate periodically but not with those of another community (Bigg et al. 1990). This multilevel society is based on distinct fission-fusion patterns of whole coherent family-based units, where stable matrilineal units collectively associate more

frequently with other close kin units. The ‘sub-pod’ and ‘pod’ were traditionally considered intermediate social levels between the matriline and the clan, consisting of matrilines with recent maternal ancestry that often (> 95% and 50% of the time, respectively) travelled together (Bigg et al. 1990; Ford 1991). However, recent studies have shown fluctuations in the reoccurrence of associations between matrilines (Ford and Ellis 2002; Parsons et al. 2009), as well as changes in the pods originally described (Ford et al. 2000), leading to suggestions that the term ‘pod’ should only be used to designate aggregations of killer whales or as a synonym for matriline (Ford and Ellis 2002).

Intraspecific variation in sociality among killer whales is believed to relate to prey-type. Northeast Pacific resident killer whales mainly prey on salmon, especially Chinook (*Oncorhynchus tshawytscha*) while mammal-eating killer whales (also referred to as ‘transients’ or Bigg’s killer whales) feed on marine mammals, especially harbour seals (*Phoca vitulina*; Ford et al. 1998). Although sympatric, these two populations comprise two specialist ecotypes that are socially and reproductively segregated (Bigg 1982; Barrett-Lennard 2000). Both ecotypes exhibit coherent and stable matrilineal social units based on long-term kinship associations but there are important distinctions between their social strategies. The resident population forms larger matrilineal units than the mammal-eating population and while the resident population is philopatric, there is some level of adult dispersal in the mammal-eating population (Bigg et al. 1990; Baird and Whitehead 2000). For example, males may disperse to briefly associate with other matrilines or live alone, randomly associating with other adult males. Moreover, some females may disperse from the matriline and stay socially mobile, associating strongly for short periods with different groups (Baird and Dill 1996; Baird and

Whitehead 2000). This variation is considered to be due to the different foraging strategies of the populations. Hunting marine mammal prey in large groups incurs greater costs by increasing the probability of detection by the prey. Furthermore, the optimal energetic intake for mammal-eating killer whales (preying upon medium-sized seals) declines for groups larger than 3 individuals (Baird and Dill 1996). In contrast, resident killer whales spread out and coordinate to locate salmon (Ford et al. 2000), potentially benefiting from larger group sizes. With little or no predation risk, populations of this species apparently refine their social systems primarily in relation to foraging efficiency, particularly availability of resources and competition for those resources.

In the North Atlantic, the only published study addressing sociality found greater similarities between the Scottish mammal-eating population and Northeast Pacific mammal-eating population relative to residents, despite greater phylogenetic distance, suggesting that ecology drives sociality more than phylogenetic inertia does (Beck et al. 2012). The study included a limited dataset from Icelandic herring-eating killer whales and their social structure was not explored in detail. However, the study's hierarchical display of associations suggested that social tiers were not clearly defined in this population and that associations at a variety of strengths existed. These features were not further addressed, nevertheless the study concluded that the Icelandic fish-eating population is probably more similar to the Northeast Pacific resident population than to mammal-eating populations.

Icelandic killer whales are believed to mainly prey upon Atlantic herring (*Clupea harengus*) and follow the Icelandic summer-spawning (ISS) herring stock during its yearly migration (Sigurjónsson et al. 1988) between overwintering, feeding and spawning grounds (Óskarsson

et al. 2009). Unlike the salmon prey of resident killer whales, herring form large and dense schools as an antipredator strategy (Nøttestad and Axelsen 1999) and killer whales feeding on herring schools use a coordinated group feeding strategy, encircling their prey to herd and capture it (Similä and Ugarte 1993). Feeding aggregations of killer whales are very common in Iceland, making it difficult to discern isolated groups and confusing the determination of associations in the field (Sigurjónsson et al. 1988; Beck et al. 2012). In addition, herring can undergo large variations in abundance and migration routes (Jakobsson and Stefánsson 1999; Óskarsson et al. 2009) making it a changeable food resource. In fact, recent research suggests not all individuals specialize on ISS herring and follow it year-round. Other killer whales observed only in one season or seasonally moving between Iceland and Scotland exhibited wider trophic niche width, suggesting diversity in foraging strategies (Samarra and Foote 2015; Samarra et al., in press; FIP Samarra et al. in prep).

In this study we investigate the social structure of herring-eating killer whales in Iceland, based upon patterns of association between photo-identified individuals in spawning and overwintering grounds. We relate our results to the described societies of killer whales in the Northeast Pacific. Specifically, we investigate: 1) the degree and diversity of associations between pairs of individuals; 2) whether social structural units of individuals exist and are hierarchically nested in the social structure; 3) how associations persist or change over time in the population and depending on age-sex class and; 4) whether variations in movement and feeding strategy within the Iceland killer whale population influence sociality by promoting social segregation. Given the differences in historical availability, migration patterns, and anti-predator strategies of herring, salmon and seals, we hypothesize that broad ecology (fish-

vs. mammal-eating) alone cannot explain sociality and that local ecological conditions, such as characteristics of prey schools and associated foraging strategy of the population, might also strongly shape the social structure of killer whales.

METHODS

Data collection

Photographs of killer whales were collected in July 2008-2010 and 2013-2015 in Vestmannaeyjar (South Iceland), a spawning ground of ISS herring, and in February-March 2013-2014 and mid-February to mid-March 2015 in Grundarfjörður and Kolgrafafjörður (West Iceland), two fjords that were part of the ISS herring overwintering grounds. During daylight hours, when killer whales were encountered, groups were approached and photographs of all individuals surfacing together were taken using a variety of digital single-lens reflex cameras with telephoto lenses. On several occasions, more than one photographer/camera was used. Sampling effort varied across years and seasons, due to weather conditions, research effort priorities, and the number of research vessels used (Table 1). In the winters of 2014-2015 a whale-watching platform was also used. Due to the inherent difficulty in approaching and photographing all individuals from whale watching platforms, only encounters when coverage of the groups present was considered complete (i.e. all individuals in the group were identified) were included in the analysis.

Photo-identification

Killer whales were individually identified based on the size and shape of the dorsal fin, patterns of the saddle patch and natural markings, such as nicks and scars, using left-side pictures (Bigg 1982). For young animals without distinct natural markings, the eyepatch was also used for identification across seasons/years. The quality of photographs was judged based upon focus, contrast, angle and overall quality assessment (adapted from Friday et al. 2000). Only high and medium quality photographs were used. To avoid false positives, matches were confirmed if 3 distinct features of the individual were unambiguously identified.

To differentiate sex and stage of maturity four different categories were used: (1) Adult males – adults that have reached sexual maturity and present distinguishable taller dorsal fin; (2) Adult females – mature size individuals, with relatively smaller dorsal fin, seen during the study period either consistently with a calf in echelon position, or without developing dorsal fin for at least 3 years, or that were matched to a preliminary catalogue from the Marine Research Institute including photos taken between 1981 and 2007, without developing dorsal fin; (3) Juveniles – identifiable individuals > 1 year old that have not reached mature size (both sexes); (4) Other – whales of apparently larger size than juveniles but for which sex and stage of maturity were impossible to determine.

Individuals that were only sighted in the summers of 2008-2010 were excluded from the analysis to reduce bias resulting from including individuals that may have died during the first years of the study and reduce the possibility of incomplete group coverage data from fieldwork where photographic data collection was opportunistic. This procedure excluded 25 individuals from the study.

Association criterion

Due to the common observations of aggregations of individuals in Iceland (Sigurjónsson et al. 1988; Beck et al. 2012), spatiotemporally isolated groups in the field are unclear and it is difficult to rigorously define a group. Despite this, the way in which animals are photographed is related to their inherent social structure, as animals that prefer to associate will undoubtedly be photographed together or in close proximity more often (Bigg et al. 1990). Using the capture time recorded in each photograph's metadata, we can discriminate animals surfacing together in close proximity, since they are photographed within a very short time frame. Individuals were considered associated for the day (sampling period) if photographed by the same camera/photographer within 20 seconds. This value was quantitatively derived by maximum likelihood estimation of photographic bouts (Langton et al. 1995; Luque and Guinet 2007; see Supplementary Material S1). The association criterion matches our field observations that groupings of adjacent associated animals tended to surface (and be available for photographing) close in time to each other and within 20 seconds, whereas non-contiguous animals were generally only available for photographing after a longer time had passed. Shorter and longer temporal association criteria (5 seconds and 1 hour, respectively) were used to test the robustness of the observed association patterns to the temporal criterion used (Supplementary Material S2). These analyses suggested that the association criterion value used in the study is likely meaningful to describe the animals' social structure and appropriate to capture important associates without overloading the analysis with random associations.

Analysis of associations

Only individuals seen on at least 5 different days were included in the analysis of associations. This value is recommended by Whitehead (2008) as a minimum cut-off and it is a more conservative restriction than several other studies (e.g. minimum cut-off of 4 sightings: Ottensmeyer and Whitehead 2003; Tosh et al. 2008; Beck et al. 2012; Esteban et al. 2016). We explored the consistency of the results under more restrictive thresholds ($\geq$ 10 days and $\geq$ 20 days; see Supplementary Material S3). Due to similarity in the obtained results and the fact that restricting the criterion for inclusion to a minimum of 5 sampling periods significantly increased the number of individuals included in the analysis, this was considered an appropriate threshold to describe the population dynamics of this social system.

All analyses described below were conducted using SOCPROG 2.6 (Whitehead 2009) in MatLab 8.5 (MathWorks, Natick, MA, U.S.A.), except where noted. To quantify associations between pairs of individuals we calculated the half-weight index (HWI), which estimates the proportion of time individuals spend together: $HWI = 2AB/(A + B)$, where AB is the number of times individuals A and B were identified associating with each other, and A and B are the total number of times each individual was identified (Cairns and Schwager 1987; Whitehead 2008a). This symmetric association index was chosen since it minimizes sampling bias when some individuals present were missed. This index was calculated per season (summer and winter) and overall.

We used a permutation test, permuting the associations within samples (days), to test whether associations in the population were different from random, with the null hypothesis that between sampling periods there are no preferred/avoided associations (Bejder et al. 1998;

Whitehead 2008a). This test reveals whether or not an observed social structure is only due to properties of the dataset used (e.g. the size of aggregations of individuals and the number of encounters or sampling periods) when the associations are not different from random. The association matrix was permuted 10000 times, when the P value stabilized, with 1000 trials (inversion of part of the matrix of associations) per permutation. The random data obtained by this process were also used in the temporal analysis of associations.

To measure how diverse the associations were, we calculated the social differentiation (*S*) of the population. Social differentiation is the estimated coefficient of variation of association indices of the population. If *S* is close to 0, the associations are very homogenous, and if $S >$ 1.0 the relationships are very diverse across dyads of animals (Whitehead 2008a; Whitehead 2009). The social differentiation was calculated using the likelihood method described by Whitehead (2008b), with non-parametric bootstrap for calculating its standard error (SE) and sampling periods chosen randomly for each of 1000 bootstrap samples.

Hierarchical stratification

Hierarchical clustering analysis using a dendogram display (tree diagram where individuals are represented by nodes and the branching pattern represents the degree of associations) have been used to visualize and interpret the social structure of killer whale populations (e.g. Bigg et al. 1990; Baird and Whitehead 2000; Beck et al. 2012). This agglomerative technique imposes a model where the social structure of the population is hierarchically structured: basic social units (permanent or semipermanent social entities at high association values) are nested

within larger social units (permanent or semipermanent social entities –'tiers' (Wittemyer et al. 2005) - at low association values) in a stratified fashion (Whitehead 2008a; Whitehead 2009).

To investigate whether or not the Icelandic population exhibits clear hierarchical stratification we combined the quantification of the distribution of HWI along with a hierarchical display of associations and a visual exploration of the stratification of the population. We displayed associations as a dendogram, using the average-linkage clustering method. To identify the association index at which significant divisions within the population occurred we used modularity, defined by Newman (2004), controlling for differences in gregariousness ('Modularity-G'; Lusseau 2007; Whitehead 2008a). To identify the degree of possible stratification among individuals we explored the fragmentation of the population's social network across lower values of HWI. We displayed the associations between individuals as a social network, where nodes represent individuals and edges (links) between nodes represent an existing association. Then, we sequentially removed edges in the population with increasing HWI values to visualize the fragmentation of the network at each level, and removed isolated (unconnected) nodes from the display for clarity. This was performed in R 3.2.3 (R Core Team 2015) using the package igraph (Csardi and Nepusz 2006).

Non-hierarchical structure and movement pattern assortative mixing

We used Newman's (2006) eigenvector-based clustering method to detect social clusters within the population. This clustering technique sequentially divides the population into

successive clusters and does not assume a hierarchical association between individuals. Maximum modularity (Q) values higher than 0.3 describe a good division of the population into clusters (Newman 2004). We described the composition, mean and maximum HWI, movement pattern of adults and social differentiation (with and without juveniles) of each cluster obtained by the division. The Pearson correlation test, calculated in MatLab 8.5 (MathWorks, Natick, MA, U.S.A.), was used to test for correlation between social differentiation and cluster size, with and without juveniles. Associations for each cluster were displayed as sociograms (circular network diagrams), created in in R 3.2.3 (R Core Team 2015) using the package igraph (Csardi and Nepusz 2006). To study the possible substructure within clusters we applied Newman's (2006) eigenvector-based clustering method to each cluster individually.

We investigated whether the different movement pattern of individuals determined association patterns by examining the assortative mixing in the population, i.e. the tendency for individuals with the same movement pattern to preferentially associate, using Newman's (2002) assortativity coefficient (r). Three different broad movement patterns were considered based on individual sighting history (as in FIP Samarra et al. in prep): (1) only identified in the winter season, (2) only identified in the summer season, (3) identified on both winter and summer seasons. This coefficient ranges from zero to one and high values of r indicate higher assortativity of the population, i.e. individuals associate only with others of the same 'type'. The assortativity coefficient was calculated in R 3.2.3 (R Core Team 2015) using the package assortnet (Farine 2014), for the whole population with and without juveniles, to account for

299 the possibility of juveniles only being identified later in the study period. The SE was
300 calculated using the jackknife method described by Newman (2003).

301

302 **Temporal patterns of associations**

303 To investigate how associations changed over time we calculated the standardized lagged
304 association rate (SLAR). All individuals, regardless of sighting frequency, were used in this
305 analysis to avoid positive bias (Whitehead 2008a). The SLAR is the estimate of the
306 probability that if two individuals are associated after a specified lag, the second individual is
307 a randomly chosen associate of the first (Whitehead 1995; Whitehead 2008a). Standard errors
308 were calculated using a temporal jackknife procedure with 15 day periods of data being
309 omitted in turn (Whitehead 1995; Whitehead 2007). To categorize how the relationships
310 between individuals changed over time, four different theoretical exponential models were
311 fitted (by maximum likelihood and binomial loss) to the full data set. The models are based in
312 the presence/absence of constant and temporary associations (Whitehead 2008a). The model
313 that best fitted the data is indicated by the lowest quasilikelihood Akaike information criterion
314 (QAIC, Whitehead 2007). The difference between the QAIC of the best model and other
315 models (ΔQAIC) indicates the degree of support for the less favored models: differences 0-2
316 indicating substantial support, 4-7 indicating less support and > 10 indicating essentially no
317 support for the alternative models (Burnham and Anderson 2002). Starting values of the
318 parameters for all models were obtained from the estimated parameters of the best-fitted
319 model in a preliminary fitting (with initial values of all parameters set to 0.5). The jackknife
320 method gives standard errors for the parameters of the model and for measures of social

structure estimated from them: typical group size (as in Jarman (1974), number of associated individuals in groups, including the individual itself) and typical unit size (number of individuals in permanent units), considering the case where permanent units temporarily group (Whitehead 2008a).

Sex differences in association patterns

Differences in patterns of association by sex were investigated as in Baird and Whitehead (2000). The mean and maximum HWI within and between sexes were calculated for adults of known sex (Females and Males) seen on 5 or more days. The mean HWI between A-B is an estimate of the probability of a random individual of category A associating with any individual of category B at any sampling period, so it is insensitive to different numbers of individuals in different categories (Baird and Whitehead 2000). The maximum HWI of A-B is the average maximum of association indices between each individual from category A and any individual from category B. We tested the null hypothesis that associations between and within sexes are similar using a Mantel test where associations between categories were permuted 5000 times (Schnell et al. 1985). Variation in temporal patterns of associations were analyzed using the SLAR for associations between all adults of known sex (Females and Males) to avoid positive bias of the SLAR.

Adult female-specific analysis

Mixing within aggregations of resident killer whales have been noted to differ between males and females: adult males can temporarily travel away from their matrilines, possibly for mating purposes (Bigg et al. 1990; Barrett-Lennard 2000), but adult females generally stay in their matrilineal units, which are spatially dispersed, particularly during foraging (Ford 1989). We therefore separately examined the associations only between the most frequently encountered adult females in the study, as they may show higher levels of association within groups and a more clearly defined tier structure than observed in the overall population. This analysis was performed using 2 restricted datasets: 1) adult females encountered on more than 10 days and at least in 3 different years; 2) adult females encountered on at least 20 days and at least in 3 different years. Permutation tests and dendograms were performed as described above, for both datasets. Associations between females were displayed in a sociogram created in R 3.2.3 (R Core Team 2015) using the package igraph (Csardi and Nepusz 2006).

RESULTS

314 individuals (88 adult males, 94 adult females, 59 juveniles and 73 others) were identified in a total of 29023 photographs taken on 110 different days. The mean ± standard deviation (SD) number of individuals identified per day was 25.1 ± 20.6 individuals (range = 1-121 total identifications per day).

Analysis of associations

198 individuals (56 adult males, 69 adult females, 41 juveniles and 32 others) were identified on at least 5 days (mean of 12.6 ± 7.1 days, range of 5-38 days) and used in the analysis of associations. 51 were only sighted in the winter season (including 8 juveniles), 32 only in the summer season (including 11 juveniles), and 115 on both seasons (including 22 juveniles). Most individuals were seen in several years (mean ± SD of 3 ± 1.5 years, range of 1-6 different years).

The mean HWI of the population was low (mean ± SD = 0.02 ± 0.01, non-zero HWI mean ± SD = 0.18 ± 0.19). Regardless of the season, the distribution of non-zero HWI values observed showed a high proportion of low level associations and relatively fewer strong ties at high HWI values (Figure 1). More than half of the pairs of associations were lower than 0.1 (51.4%, 1161 dyads). Only 9.9% (224 dyads) of the associations had HWI $\geq$ 0.5 (individuals associated more than half of the time). This was the value used by Baird and Whitehead (2000) to define matrilines in the Pacific mammal-eating population and by Bigg et al. (1990) to define pods of matrilines that frequently associated. Only 0.9% of the associations (21 dyads) were higher than 0.8, the value used by Beck et al. (2012) to define primary social tiers, equivalent to matrilines.

The SD and coefficient of variation (CV) of association indices were significantly higher in the real dataset than in the permuted data (real SD = 0.09, random SD = 0.05, P=0.0001; real CV = 4.12; random CV = 2.59; P = 0.0001). Hence, we could reject the null hypothesis that individuals associated randomly. The social differentiation of the population was close to 1 (*S* ± SE = 0.98 ± 0.03), revealing a highly diverse range of associations within the population.

382

383 **Hierarchical stratification**

384 Applying the hierarchical dendogram display (cophe

385 netic correlation coefficient [CCC] > 0.8; Figure 2), social clusters diverged at an extremely
386 low association index value (HWI of 0.02, maximum modularity of 0.68). The knot diagram
387 presented an apparent constant rate of cumulative bifurcations, which only slightly increased
388 at very low association indices. This pattern was still visible using a very restrictive
389 association criterion (Figure S3 in Supplementary Material S2). The network of associations
390 was more interconnected at low HWI thresholds (Figure 3). However, without a larger
391 number of strong bonds the network started to fragment very quickly when links were
392 sequentially removed at low HWI thresholds. The network contained few stronger ties, as is
393 visible when HWI = 0.5, with very small sets differentiated and individuals detached from the
394 network. Associations in the Icelandic killer whale population did not appear to be clearly
395 stratified into hierarchical tiers. Considering the wide range of association levels present, this
396 does not mean that individuals only associate with a small set of companions.

397

398 **Examination of structure and movement pattern assortative mixing**

399 Using Newman's (2006) clustering technique, the population could be significantly divided in
400 18 distinct clusters (Table 2; Q = 0.66). The social clusters obtained in the analysis were of
401 mixed sex-age classes. The cluster sizes varied between 3 and 33 individuals, with a mean ±
402 SD of 11 ± 7.8 individuals per cluster. As expected, mean HWI within clusters was higher

403 than between clusters (within clusters mean HWI ± SD = 0.27 ± 0.17 and maximum HWI ±
404 SD = 0.65 ± 0.17; between clusters mean HWI ± SD = 0.01 ± 0.01 and maximum HWI ± SD
405 = 0.01 ± 0.06). The assortativity coefficient of the network indicated some level of separation
406 of associations according to movement pattern (including juveniles r ± SE = 0.44 ± 0.01; not
407 including juveniles r ± SE = 0.49 ± 0.01) but much lower than would be expected if
408 individuals favored associations with others of equal movement pattern and/or avoided
409 associations with individuals with a different movement pattern. In fact, not all clusters were
410 discriminated by movement pattern: 5 clusters were composed of a mix of individuals sighted
411 in both seasons and individuals sighted in a single season.

412 Clusters were highly variable in their complexity (Table 2). There was a wide range of values
413 of social differentiation by cluster (with juveniles mean ± SE = 0.52 ± 0.1, min-max: 0-1.15;
414 without juveniles mean ± SE = 0.49 ± 0.1, min-max: 0-1.17). The Pearson's correlation test
415 showed that social differentiation was significantly correlated with unit size (with juveniles r
416 = 0.68, P = 0.002; without juveniles r = 0.62, P = 0.006). Within larger clusters not all
417 associations were strong (representing high social preference) or weak, and members
418 associated at many different degrees. In general, only a few individuals within each cluster
419 maintained strong associations (> 0.5 or 0.8) with other members and only 5 clusters had a
420 mean HWI > 0.5. From the measures of social structure, inspection of photographs and direct
421 observations we concluded that we were not able to identify all companions of the members
422 of cluster F. This cluster was most likely incomplete and therefore was not included in further
423 descriptions.

Our analysis distinguished three types of social clusters in the population: stable (C, G, K, N, O and P; Figure 4), intermediate complexity (D, H, M, Q and R; Figure 5) and complex (A, B, E, I, J and L; Figure 6) clusters. Stable clusters had high mean HWI values, very low social differentiation and members with equal movement pattern. Only in cluster G two juveniles were subclustered with a very low modularity value, likely because they were born during the study period and only identified later in the study. Therefore, these clusters had no apparent substructuring and associations between members were generally more homogeneous but not equal.

Intermediate complexity clusters had intermediate values of mean HWI and social differentiation, showing potential but unclear subclustering (Q values generally < 0.3), since individuals across potential subclusters also associated very frequently. In general, cluster members had equal movement patterns, except for one cluster.

Complex clusters had very high values of social differentiation and very low mean HWI, but high maximum HWI. In general, cluster members had different movement patterns, except for two clusters. Complex clusters showed potential substructuring, although this was not clear for all clusters (Q values of about 0.3 for cluster B and J). Associations between members of complex clusters were diverse and only some members maintained strong associations, with most associations being lower and at varying levels.

Temporal patterns of associations

The standardized lagged association rate SLAR ($g'(\tau)$) remained higher than would be expected from random associations over the investigated time periods (τ; Figure 7), indicating that non-random associations persisted over time.

The two more complex models presented a reasonable fit to the data (see Supplementary Material S4). The model SLAR3, labelled as 'constant companions plus casual acquaintances' in Whitehead (2008a), had the lowest QAIC value, fitting the data best. Adding a second level of dissociation (SLAR4), gave a similar curve and a very small difference of QAIC to SLAR3 indicating some support for this model. However, contrary to SLAR3, there was no convergence and stable fit of SLAR4 when varying the parameters start values, which raised doubt on the suitability of this model for the data. For this reason the simpler model SLAR3, which has lowest QAIC and consistent parameters, was chosen to describe the temporal patterning of associations. This model indicated that the population was driven by a combination of longer-term relationships that last for many years, and temporary associations: $g'(t) = 0.06 + 0.02e^{-0.0486t}$. Temporary associations decayed exponentially, with the model suggesting important dissociations over scales of about 21 days (0.0486/days, SE = 0.09). The proportion of long-term associations was 77%, with only 23% of temporary relationships. This model's fit estimated a typical group size of 14.8 individuals (SE = 2.5) and a typical unit size of 11.7 individuals (SE = 3.4).

Sex differences in association patterns

125 adults of known sex seen on 5 or more days were used in this analysis. Association levels within and between adult sex classes were similar, with low mean association indices and high maximum association indices (Table 3). The Mantel test did not reveal clear significant differences in association between, relative to within adult sex classes (permutation test, P = 0.05). If the analysis was restricted to 75 adults of know sex seen on more than 10 days there was no significant difference in association (permutation test, P = 0.13). The temporal analysis suggests that Female-Male, Male-Male and Female-Female associations were somewhat stable across time and remained higher than random (Figure 8). For all types of associations, the SLAR was higher than the SLAR between all individuals (higher probability of association). In general, all SLAR were relatively stable over time and no sex difference was noticeable.

Adult female-specific analysis

32 adult females were sighted on more than 10 days over at least 3 years and only 12 of those were sighted on at least 20 days over at least 3 different years (Table 4). On both restriction conditions, associations were non-random (32 females: real SD = 0.11, random SD = 0.08, P = 0.0001 and real CV = 2.33, random CV = 1.72, P = 0.0001; 12 females: real SD = 0.17, random SD = 0.14, P = 0.0001 and real CV = 1.51, random CV = 1.31, P < 0.0001). The classical hierarchical clustering technique displayed dendograms with a varying level of associations between females, with significant clusters discriminated at low HWI values (see Table 4 and Supplementary Material S5). Although the cluster discrimination occurs at a higher HWI value for the set of females with the more restrictive observational threshold, it is

still a low value and mostly weak associations are present within the discriminated clusters. The sociogram showed that, regardless the observational threshold, associations between females are mainly weak even between most females from the same cluster (Figure 9). Also, there are several weak associations between females from many different clusters.

DISCUSSION

Our results showed that associations within the Icelandic population of herring-eating killer whales were non-random but the number of strong associations was small. Although the dendogram display of associations presented a high cophenetic correlation coefficient, social clusters were differentiated at extremely low levels of association. With this technique, individuals were clustered together also by least preferred associations, i.e. weaker associations at very low HWI values, since not all individuals associated strongly within social units.

In a hierarchically structured society, transitions between structural tiers are clear because individuals within a social cluster (nested in a tier) associate more strongly than individuals within clusters at the level above. Societies without hierarchical nesting can still display a dendogram with a cophenetic correlation coefficient > 0.8, indicating an acceptable match to the matrix of association indices (Bridge 1993), while being an inappropriate way of realistically displaying associations (Whitehead 2008a; Whitehead 2009). When individuals associate weakly overall the degree of potential hierarchical stratification is limited since an individual cannot represent its social unit because associations within a social unit are not

equally strong. Our study showed this to be the case in this population. Thus, a non-stratified way of studying the society was considered more appropriate than techniques that assume a hierarchically-organized social structure.

The population could be significantly divided into social clusters, which were highly diverse in complexity (even when using a more restrictive observation threshold; Supplementary Material S3 – Figure S10). A small portion of the clusters presented more coherent associations between members, which might represent cohesive basic structures. The majority of the clusters presented diverse association strengths and potential further subclustering. In some social clusters, many individuals did not strongly associate with all other members. This population presented both constant and temporary associations, not completely assorted by movement pattern and with no clear differences between sexes. Together these results suggest that the Icelandic herring-eating killer whale population has a multilevel society with no clear nested hierarchical structure of coherent social units, different from other populations of killer whales studied to date.

The evidence for non-random associations indicates that our results were not merely a consequence of the quality or constraints of the dataset. It is possible that some of the HWI values were negatively biased due to incomplete photographic coverage of groupings/aggregations (Ottensmeyer and Whitehead 2003). However, this type of bias would only increase the probability of not rejecting the null hypothesis of associations being random. The analysis using the most encountered adult females aimed at reducing the potential influence of recording sporadic associations, due to the observation that adult female resident killer whales have lower levels of mixing with other groups than other age-sex classes. Thus,

a matrilineal structure may have been more clearly detectable among adult females than in the overall population. However, our population-level results were instead strongly supported by the adult female-specific analysis, with adult females also presenting an unclear hierarchical structure but a complex sociality with rare strong associations and many weak associations between females from the same cluster, and several associations between females from different clusters. There are indications that the weakness of associations is due to a high variability across years (associations on one year might not occur in a different year) but the small yearly number of sightings limits our ability to reach a definitive conclusion on the stability of associations and yearly preferences between these individuals.

A complex multilevel society

In the Icelandic herring-eating killer whale population individuals clearly associated at different levels, in some cases forming subcluster units. This society appears to tend towards an incompletely nested multilevel society (as in Figure 6 in de Silva and Wittemyer 2012). The levels of social stratification are not hierarchically distinct because transitions between levels are gradual and may vary among individuals or sets of individuals, i.e. not all individuals associate at similarly higher levels within social units and at distinctly lower levels between social units. The variability in cluster complexity indicates diverse association patterns among individuals and suggests different association strategies within the population.

Killer whale movement patterns did not assort their associations. In fact, individuals from different subclusters and clusters with markedly different movement patterns were commonly

550 seen in tight groupings within less than one body length, a measure commonly used in other
551 killer whale social structure studies to define a group (e.g. Ivkovich et al. 2010, Esteban et al.
552 2016; Figure 10). Furthermore, complex cluster A (Figure 6) was formed by 3 highly
553 distinctive subclusters: subcluster A1, composed of individuals seen in Iceland year-round
554 following the movements of the ISS herring stock; subcluster A2 composed of individuals
555 that are only seen in Iceland in the winter; subcluster A3, composed of 5 individuals matched
556 to the Scottish population (only 2 Others and 1 Juvenile from this cluster were not matched)
557 and sighted in Scotland in the summer (Samarra and Foote 2015). Combining social structure
558 analysis with genetics could help to clarify the underlying aspects of social contact reported
559 here between whales with different movement patterns and potentially different feeding
560 ecologies in Iceland. It is worth noting that the individuals matched to the Scottish population
561 were not always sighted together in Scotland (Samarra and Foote 2015) nor in Iceland. It is
562 possible that individuals were missed in Scotland due to the opportunistic nature of data
563 collection. However, in our study we could confirm that these individuals were not always
564 associating at close proximity.

565 The Icelandic multilevel society seems to be driven by a mix of both constant and temporary
566 associations of mean duration of about 21 days. This temporal pattern of fission-fusion
567 dynamics can occur in several types of social systems: 1) one in which constant permanent
568 social units temporarily associate; 2) one in which individuals temporarily maintain casual but
569 preferred associations and; 3) one in which permanent units exist but some individuals are
570 ‘floaters’ who move between units (Whitehead 2008a). When full units of individuals
571 collectively join, the typical group size should be twice the typical unit size, as in Pacific

572 sperm whales representing 2 temporal stable units joining (Whitehead et al. 1991) or larger, as
573 in Nova Scotia long-finned pilot whales where a group is comprised of several units
574 (Ottensmeyer and Whitehead 2003). Our study suggests that the temporal pattern did not
575 result from permanent social units temporarily associating since the estimated typical group
576 size was less than double of the typical unit size. Also, there was no indication of 'floaters'
577 moving between units and no evidence of adult dispersal in the Icelandic population. Instead,
578 temporary associations are probably formed between preferred but casual associates or
579 potentially by small sets of associates who temporarily associate with full permanent units, as
580 small sets of associated 'floaters'. Cluster members with weaker ties might represent these
581 casual but preferred temporary associates. It is unknown if this behavioral flexibility is only
582 maintained when killer whales aggregate in herring grounds or if it is seasonally shaped, so
583 further studies will be necessary to understand this type of affiliation.

584

585 **How can local ecological context shape killer whale social structure?**

586 Methodological differences among studies (e.g. disparity in sampling procedures, definition
587 of association, association index used) prevent a quantitative comparison of social structure
588 between the Icelandic and other killer whale populations. Nevertheless, overall social
589 structure comparisons can still be made. If sociality was determined by fish- vs. mammal-
590 eating ecological differences alone (Beck et al. 2012), we would expect that the Icelandic
591 population would have a similar social structure to fish-eating resident killer whales. Indeed,
592 mammal-eating killer whales show dispersal of either sex from maternal groups and relatively
593 rare and unstable associations between adult males (Baird and Whitehead 2000) which we did

not observe in our study and is also not present in residents (Bigg et al. 1990). These specific characteristics of the mammal-eating population are linked to optimal foraging group size adjustment when feeding on seals (Baird and Dill 1996). However, the clear stable matrilineal units (cohesive long-term groups) with members associating strongly and permanently (Bigg et al. 1990; Baird and Whitehead 2000) common to both mammal-eating and residents, was not found in the Icelandic herring-eating population.

Coherent basic social units have been described for other killer whale populations regardless of targeted prey (in Alaska: Matkin et al. 1999; Marion Island: Tosh et al. 2008; Northwest Pacific: Ivkovich et al. 2010; and Gibraltar: Esteban et al. 2016) and it has been considered a firm characteristic of the species despite ecological differences. In the Icelandic herring-eating population the possible existence of matrilineal units is not clear, but cannot be rejected. For example, the potential subclustering of cluster D (Figure 5) is matched to direct observations of constant close proximity associates, which could be more similar to basic matrilineal units. Yet, these subclusters were still strongly associated and were seen frequently switching preference for close companions across days and years, as well as with individuals from other clusters. Therefore, if matrilineal units are present in this population it is possible that these are not entirely comparable to the ones present in other killer whale societies. An increase in the timespan of association data and genetic analysis, relating kinship and gene flow with the underlying patterns of associations, will be crucial to inform on the presence and characteristics of family bond-units in this population.

Further differences from the resident killer whale society were the lack of clear social tiers and hierarchical nesting in the Icelandic herring-eating society, which included fission-fusion

616 dynamics at an individual (or sets of a few individuals) rather than at a group level (periodic
617 merging of permanent social units). A parallel variation in multilevel structuring has been
618 quantified in elephant societies (de Silva and Wittemyer 2012). African elephants (*Loxodonta*
619 *africana*) maintain a clear multitiered society of coherent basic units that associate
620 hierarchically. In contrast, Asian elephants (*Elephas maximus*) have a complex multilevel
621 society without hierarchical structuring and nested units. Asian elephants do not maintain
622 clear core groups and associations can be either ephemeral or long-term. de Silva and
623 Wittemyer (2012) could not determine whether these differences were due to phylogenetic or
624 ecological factors, but there were significant environmental differences between the two
625 societies, such as differences in primary productivity and predation pressure.

626 Our study points to a different view of killer whale social structure, with a more dynamic and
627 fluid sociality than generally inferred from broad ecology. As argued by Beck et al. (2012),
628 ecology probably influences killer whale sociality rather than simply phylogenetic separation
629 of populations. However, considering only fish- vs. mammal-eating strategies as the
630 ecological condition influencing sociality ignores important particularities of local ecological
631 context. Herring-eating killer whales in Iceland target a prey with particular characteristics
632 different from salmon and seals, such as antipredator behaviors, unpredictability and patchy
633 distribution of high biomass. This shapes the feeding behavior of the population and probably
634 its social structure.

635 Herring is a schooling fish with a diverse repertoire of antipredator maneuvers (Nøttestad and
636 Axelsen 1999). Feeding upon this prey requires a highly coordinated group feeding technique
637 to herd and catch herring (Similä and Ugarte 1993), unlike feeding techniques described for

other fish-eating killer whale populations. To efficiently hunt larger concentrations or school sizes using a coordinated foraging technique, killer whales might benefit from larger group sizes to encircle the herring school (Vabø and Nøttestad 1997; Nøttestad et al. 2002). Active adjustment of killer whale numbers hunting herring schools has been observed in Norway (Nøttestad et al. 2002): on 4 observations of feeding groups (range of 22-46 individuals, mean ± SD = 33.5 ± 10.6 individuals), the 2 largest groups (38 and 46 individuals in total) occurred when the herring layer was larger (depth range of 150/160 meters to 350 meters) and were composed by different smaller groups of killer whales that gathered before starting to herd herring, arriving from different directions. In these conditions, it might be important to maintain a fission-fusion society where associations are flexible and individuals can actively adjust to these constantly changing requirements.

Herring can also undergo substantial changes in density and spatial distribution, particularly in overwintering grounds (Óskarsson et al. 2009). The unpredictability of the prey may additionally promote the maintenance of a more fluid and flexible sociality. A socioecological model proposed for dolphins suggests that when resources are unpredictable, dolphins will present wide range movements, reduced competition by cooperative foraging and larger groups to more effectively find and exploit large prey schools (Gowans et al. 2007). Dusky dolphins (*Lagenorhynchus obscurus*) in Argentina feed on schooling fish and present similar basic herding techniques to herring-eating killer whales (Würsig and Würsig 1980). Their target prey is also unpredictably distributed. The population presents a strong fission-fusion society with constantly fluctuating subgroup memberships (although some associations might be constant) that split for feeding and social purposes (Würsig and Würsig 1980; Würsig and

660 Bastida 1986). This social structure is very different from dusky dolphins of New Zealand
661 (Markowitz 2004), whose target preys are more predictable.

662 Finally, feeding aggregations in Iceland are very common during summer and winter, in
663 grounds where herring are temporarily highly concentrated. The patchiness of a resource will
664 influence whether animals do aggregate and, although these aggregations for feeding are not
665 social structures (spatiotemporal clusters of individuals forced by non-social factors) they
666 might act as catalysts for sociality (Whitehead 2008a). Recurring aggregations due to prey
667 behavior may offer a special local ecological context for the establishment of associations,
668 creating opportunities for social interactions with other individuals and somehow shaping the
669 social structure of this population. The dynamic nature of the society described here may have
670 been uncovered because our data collection took place mostly during periods when large
671 aggregations of whales can occur, due to this particular ecological context. Future work
672 focusing on social associations of herring-eating killer whales during periods when herring
673 are more dispersed may reveal stronger social bonds, and clear long-term stable matrilineal
674 groups, if group sizes are substantially lower than observed during the herring spawning and
675 overwintering periods.

676 Other ecological differences such as habitat characteristics or historical capture might have
677 also shaped the social structure of this population but we lack sufficient information to
678 determine their influence at present. Furthermore, the Icelandic population is comprised of
679 individuals with different seasonal movement patterns that associate at least seasonally. This
680 alone can influence the social structure of the population, since different movement patterns
681 within the same population suggest exposure to different environmental conditions. This

might also lead to variation in social factors within the population, e.g. mating competition or avoidance, which can influence the structuring of basic and high-order groups in mammals (Silk 2007). More information on the genetic relatedness of whales with different movement patterns is needed to understand how it may affect the resulting society.

We have shown that the Icelandic herring-eating killer whale population has a complex multilevel social structure with no clear hierarchical nesting and no strong social segregation by movement pattern. This social system appears to be different from other populations of killer whales worldwide, but continued photo-identification data will be crucial to investigate these questions over longer time scales and under different seasonal, spatial and prey behavioral contexts. The differences observed suggest that fish vs. marine mammal prey-type alone does not define killer whale social structure and local ecological context, such as prey characteristics and foraging strategy, are probably strong drivers of sociality. The factors constraining hierarchical stratification of societies are little understood and to our knowledge are not addressed in socioecological frameworks (e.g. Emlen and Oring 1977; Wrangham 1980; Gowans et al. 2007). Comparative studies of populations targeting similar prey will be extremely important to quantitatively assess the degree of variation in multilevel social structuring with local ecological context.

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Data accessibility statement

Analyses reported in this article can be reproduced using the data provided by Tavares et al. (2016).

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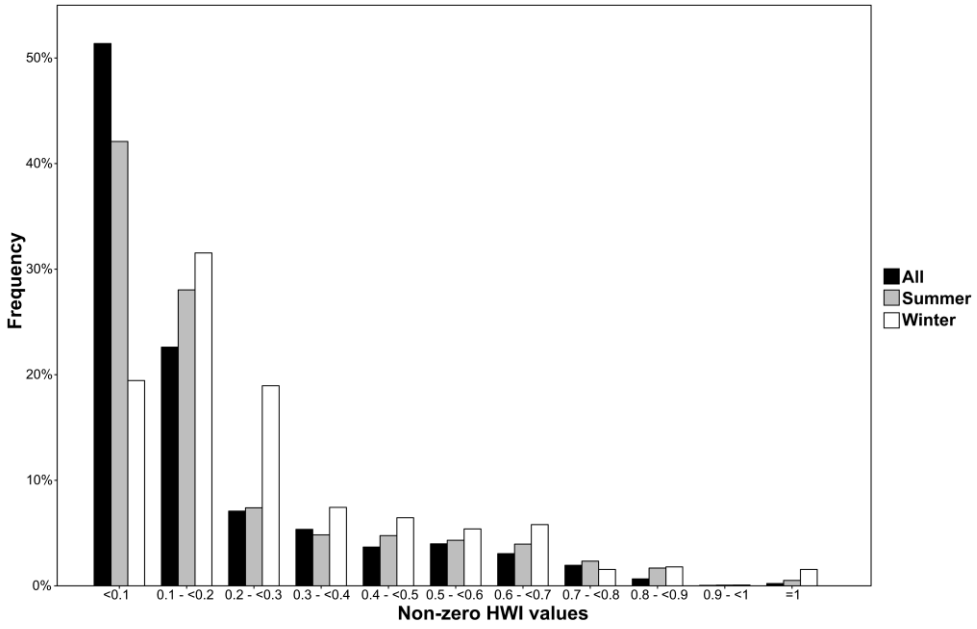
862 **FIGURE LEGENDS**

863

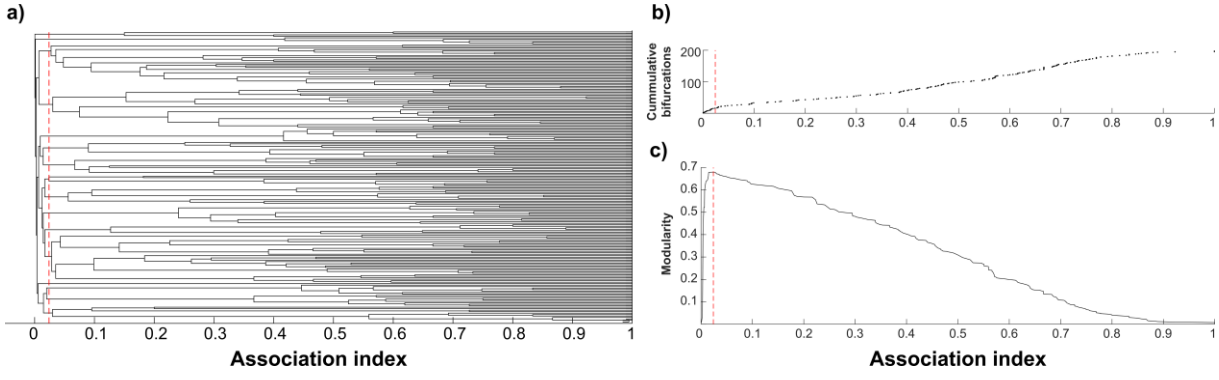


864

865 Figure 1. Distribution of non-zero half-weight index (HWI) values in the population using the

866 full dataset and by season.

867



868

869 Figure 2. Average-linkage cluster analysis. (a) Dendogram of 198 individuals encountered on

870 at least 5 days (cophenetic correlation coefficient [CCC] = 0.94). (b) Knot diagram of

cumulative number of bifurcations across HWI levels. (c) A maximum modularity-G, within hierarchical clustering, of 0.68 suggests a division into distinct clusters at an HWI of 0.02 (dashed line).

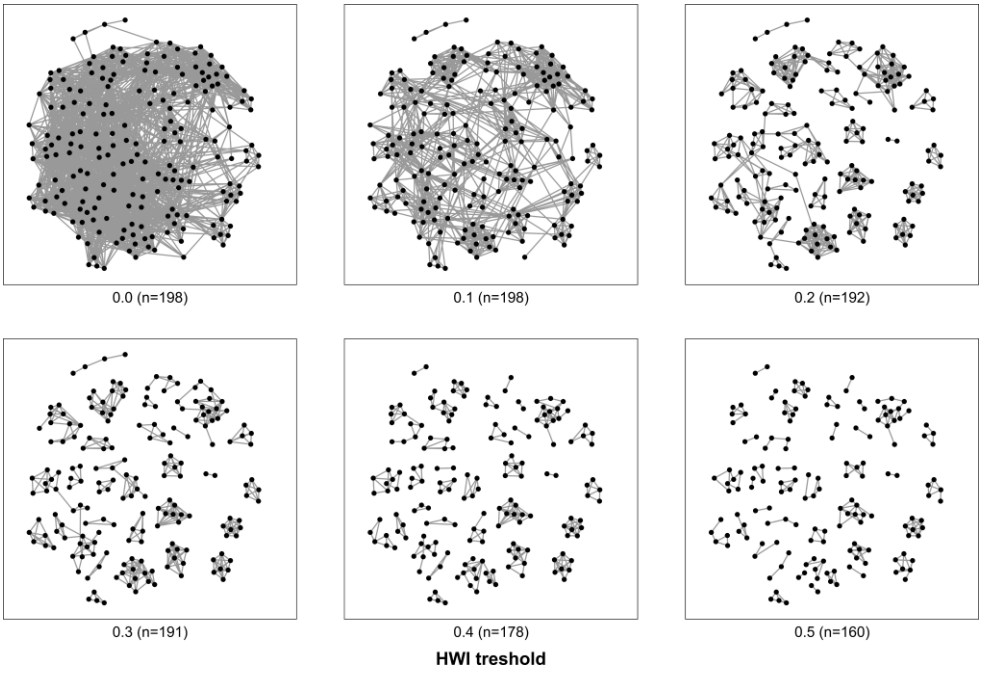


Figure 3. Network fragmentation with increasing HWI threshold. Isolated individuals are removed from the network (n indicates the number of individuals present). Note that at HWI > 0.1 the network starts fragmenting quickly and more individuals become isolated from the network. Plotted using Fruchterman-Reingold force-directed layout (Fruchterman and Reingold 1991).

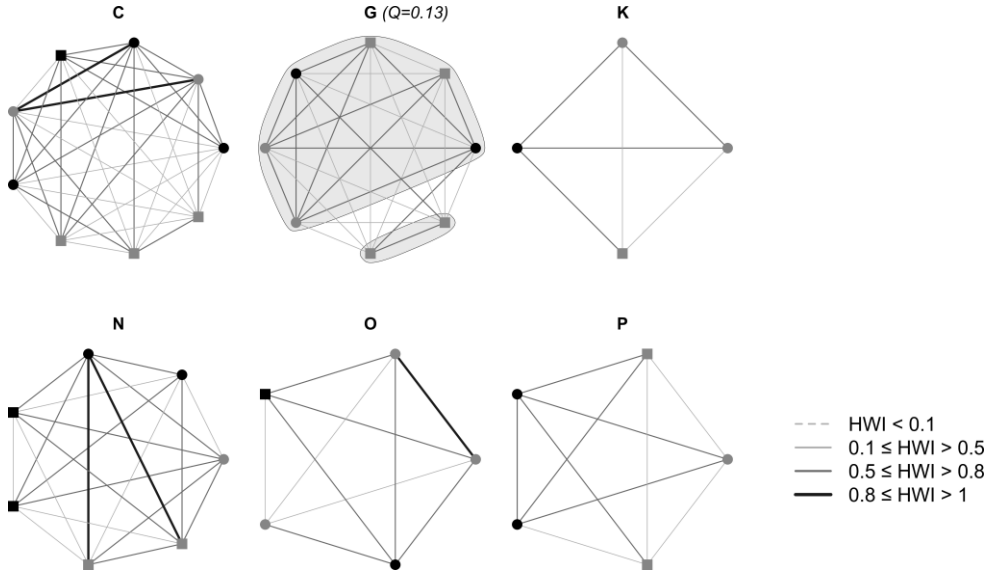
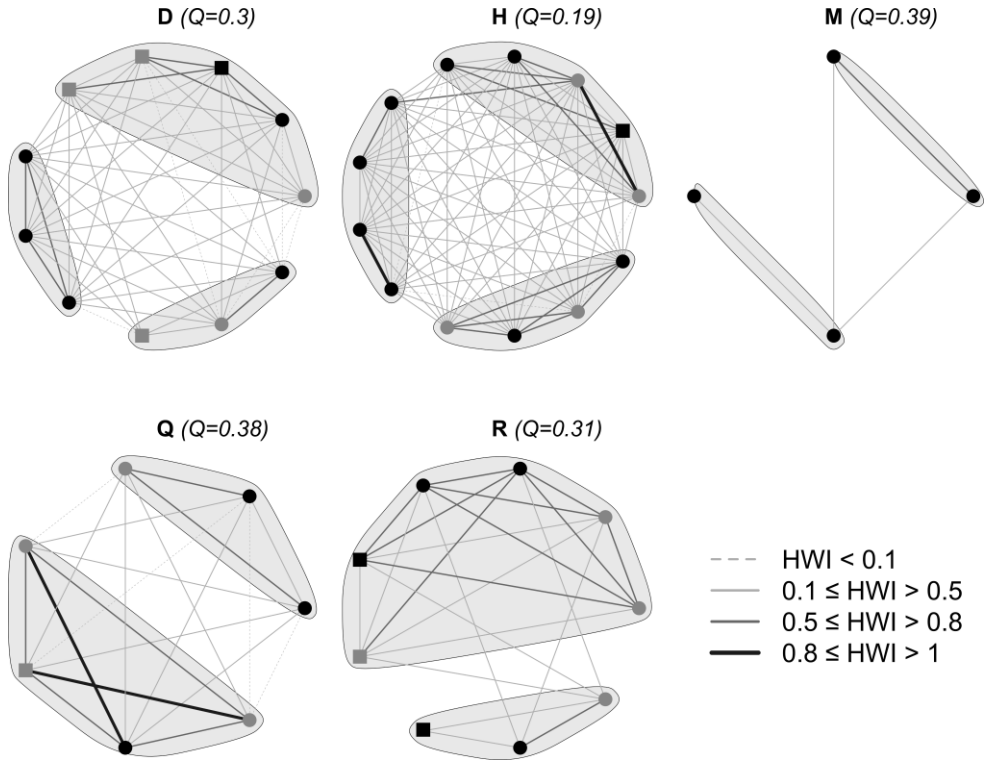


Figure 4. Sociogram of stable clusters. The thickness of the edges is related to the HWI value of association. Nodes represent individuals and are shaped/colored based on age-sex class (black circle: Female; grey circle: Male; black square: Other; grey square: Juvenile). There was no apparent subcluster division. Two juveniles were subclustered in cluster G but with a very low modularity value (Q), likely because the juveniles were only identified on the later years of the study, contrary to other members.



890

891 Figure 5. Sociogram of intermediate complexity clusters. The thickness of the edges is related
892 to the HWI value of association. Nodes represent individuals and are shaped/coloured based
893 on age-sex class (black circle: Female; grey circle: Male; black square: Other; grey square:
894 Juvenile). Q indicates the modularity of potential subcluster division.

895

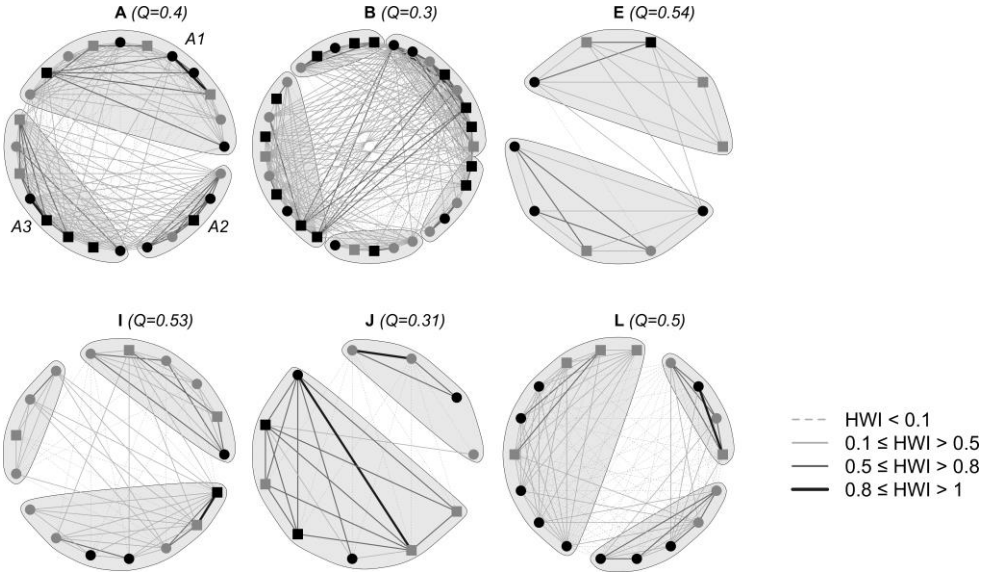


Figure 6. Sociogram of complex clusters. The thickness of the edges is related to the HWI value of association. Nodes represent individuals and are shaped/colored based on age-sex class (black circle: Female; grey circle: Male; black square: Other; grey square: Juvenile). Q indicates the modularity of potential subcluster division. A1, A2 and A3 indicate the 3 subclusters of Cluster A.

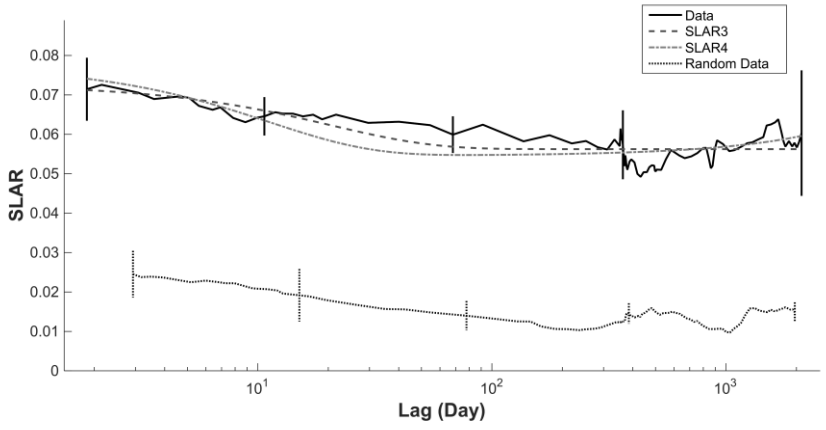
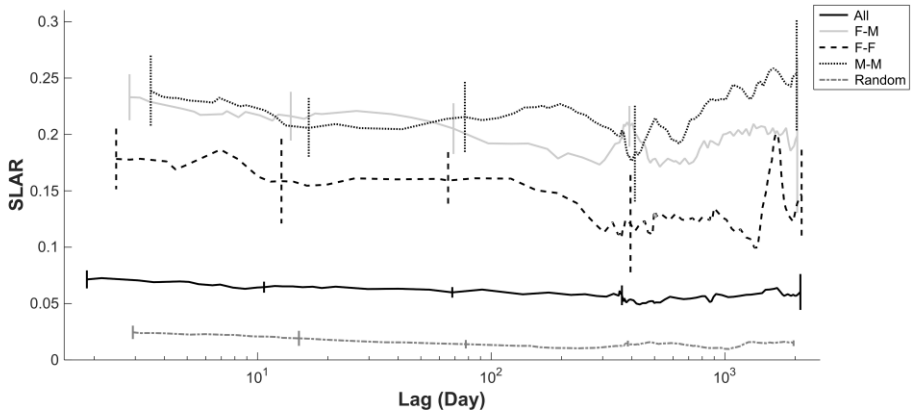


Figure 7. Standardized random and lagged association rates (SLAR, curve smoothed with 30000 moving average). Vertical bars represent temporal jackknife standard errors. The two

906 models of the exponential family with the lowest QAIC values, SLAR3 and SLAR4, are
907 shown (see Supplementary Material S4 for formulas and QAIC values).

908



909

910 Figure 8. Standardized lagged association rates (SLAR) for different associations between
911 adults. A different moving average was chosen accordingly to smooth lines. Jackknife
912 grouping factor of 15, shown as vertical bars. SLAR between Females and Males (F-M) and
913 between Males and Males (M-M) are high and relatively stable. Although lower, SLAR
914 between Females and Females (F-F) are also high and much higher than the SLAR between
915 all individuals (All) or if individuals had a random chance of associating (Random).

916

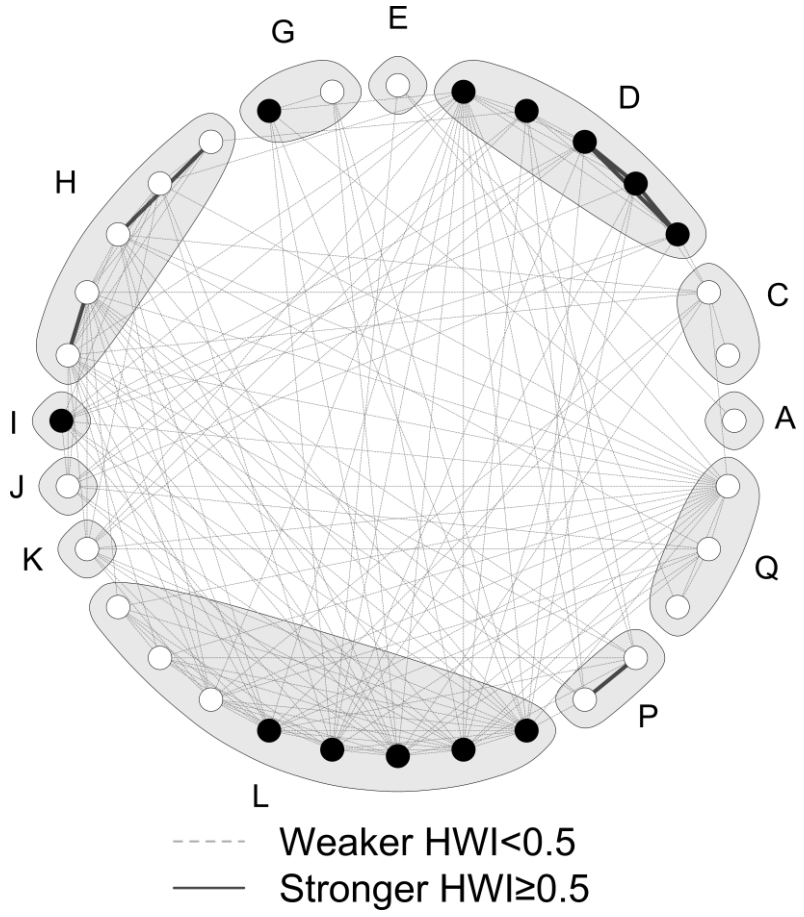


Figure 9. Sociograms of associations for the 32 most frequently encountered adult females (on more than 10 days over at least 3 years) from 12 different clusters. Nodes represent each female and are colored black if the individual was also seen on at least 20 days over at least 3 different years. Members of the same cluster were included within the same grey shading. Note the lack of strong associations and that there are many weak associations between females from different clusters. This is observed regardless of the minimum number of sightings, with predominantly weak associations across black nodes.

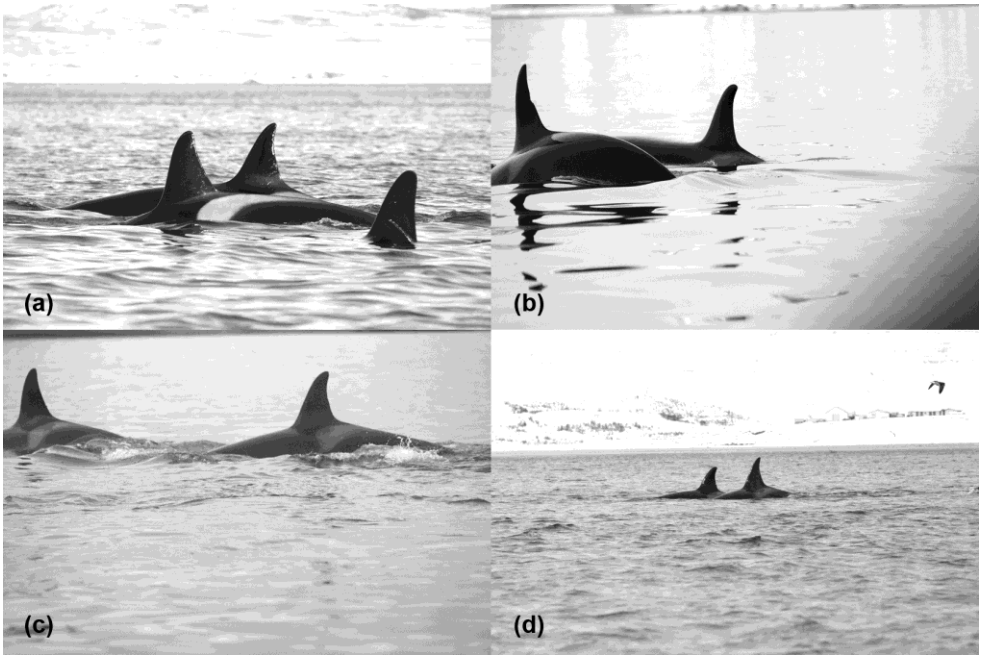


Figure 10. Examples of close associations between individuals from different subclusters and clusters: (a) IF-4 (Female, subcluster A3, Scotland ID 21) in close association with IS121 (Other, subcluster A1); (b) 997 (Female, subcluster A3, Scotland ID 19) in close association with IS041 (Female, cluster L); (c) IS172 (Other, subcluster A3) associating with IS049 (Female, cluster D); (d) IS229 (Other, subcluster A3) associating with IS030 (Female, cluster D).

933 **TABLES**

934 Table 1

935 Summary of the photo-identification sampling effort included in this study.

		Sampling periods used (days)			Number of	
Year	Season	Research vessels	WW platform	Start-end of sampling periods	Photographs	Identified individuals
2008	Summer	6	-	8th – 20th July	382	29
2009	Summer	16	-	7th – 29th July	2552	65
2010	Summer	6	-	4th – 10th July	748	70
2013	Winter	23	-	10th February – 24th March	5649	211
	Summer	4	-	17th – 29th July	1980	51
2014	Winter	19	1	13th February – 31st March	5510	115
	Summer	15	-	6th – 27th July	5265	149
2015	Winter	-	1	1st March	118	3
	Summer	19	-	7th – 29th July	6819	131

936 Days of sampling are discriminated by type of platform: research vessels and whale-watching (WW) boat.

Table 2

Summary of different clusters identified using Newman's (2006) clustering technique.

Cluster	n	Movement pattern[1]	Days	Identifications[2]	Mean HWI (SD)	Max HWI (SD)	*S* (SE)	*S* (SE) excluding juveniles
A	24 (5)	WB	34	2279	0.178 (0.04)	0.67 (0.15)	0.88 (0.1)	0.85 (0.1)
B	33 (3)	W	31	4112	0.12 (0.06)	0.62 (0.15)	1.01 (0.04)	1.01 (0.04)
C	9 (3)	B	15	798	0.54 (0.09)	0.73 (0.11)	0.08 (0.12)	0.05 (0.13)
D	11 (3)	B	60	3883	0.27 (0.06)	0.65 (0.13)	0.66 (0.06)	0.57 (0.08)
E	10 (4)	WB	24	549	0.2 (0.04)	0.55 (0.14)	0.96 (0.05)	0.86 (0.08)
F	3	B	10	91	0.12 (0.05)	0.18 (0)	0 (-)[3]	-
G	8 (4)	B	27	1918	0.49 (0.07)	0.67 (0.08)	0.17 (0.11)	0 (0.07)
H	13	B	31	1817	0.34 (0.04)	0.74 (0.07)	0.36 (0.12)	-
I	17 (4)	SB	65	2754	0.13 (0.05)	0.56 (0.19)	1.15 (0.03)	1.17 (0.04)
J	11 (3)	SB	33	1344	0.31 (0.16)	0.81 (0.25)	0.95 (0.06)	1.08 (0.05)
K	4 (1)	S	19	675	0.6 (0.08)	0.69 (0.08)	0 (0.11)	0 (0.03)
L	18 (5)	B	54	2825	0.16 (0.02)	0.59 (0.15)	1 (0.06)	0.91 (0.1)
M	4	B	8	142	0.27 (0.09)	0.5 (0.12)	0.47 (0.32)	-
N	7 (2)	SB	9	464	0.54 (0.08)	0.73 (0.1)	0 (0.19)	0 (0.12)
O	5	B	8	456	0.6 (0.1)	0.74 (0.12)	0 (0.2)	-
P	5 (2)	B	22	680	0.53 (0.09)	0.68 (0.11)	0.17 (0.09)	0 (0.09)
Q	7 (1)	B	31	1137	0.37 (0.1)	0.75 (0.13)	0.67 (0.14)	0.68 (0.14)
R	9 (1)	B	18	511	0.28 (0.13)	0.64 (0.18)	0.79 (0.09)	0.86 (0.09)

n, number of members with number of juveniles in brackets; HWI, half-weight index of association; SD, standard deviation; *S*, social differentiation; SE, standard error.

[1] Movement pattern of non-juvenile members: W – only seen in the winter, S – only seen in the summer, B – seen in both seasons, WB – seen only in the winter or in both seasons, SB – seen only in the summer or in both seasons.

[2] Total number of photographic record of identified individuals of each cluster.

[3] There was insufficient association data to calculate SE of *S* for Cluster F.

945 Table 3

946 Distribution of HWI for adult individuals seen at least 5 times, between and within sex

947 classes.

Adult sex classes	Mean HWI (SD)	Max HWI (SD)
Females-All	0.02 (0.01)	0.59 (0.18)
Males-All	0.02 (0.01)	0.62 (0.21)
Females-Females	0.02 (0.01)	0.44 (0.21)
Females-Males	0.02 (0.01)	0.48 (0.24)
Males-Females	0.02 (0.01)	0.56 (0.23)
Males-Males	0.02 (0.01)	0.48 (0.26)
Within classes	0.02 (0.01)	0.46 (0.24)
Between classes	0.02 (0.01)	0.52 (0.23)
All-All	0.02 (0.01)	0.6 (0.19)

948 HWI, half-weight index of association; SD, standard deviation.

949 Table 4

950 Summary of the results of the adult female-specific analysis under two different observational
951 thresholds.

Observational threshold	**> 10 days, ≥ 3 years**	**≥ 20 days, ≥ 3 years**
n	32	12
Mean ± SD sightings	19.1 ± 6.6 days (range of 11-34 days) over 4.6 ± 1 years (range of 3-6 years)	26.3 ± 4.5 days (range of 20-34 days) over 5.3 ± 0.5 years (from 5-6 years)
Non-random associations?	Yes	Yes
Dendogram	Figure S10 - Supplementary Material S5	Figure S11 - Supplementary Material S5
Divergence of clusters at HWI	0.04	0.21
Modularity	0.48	0.39

952 n, number of adult females in the analysis; HWI, half-weight index of association; SD, standard deviation.